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Stand-Level Gas-Exchange Responses to Seasonal Drought in Very Young Versus Old
Douglas-fir Forests of the Pacific Northwest, USA

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1 **Summary**

2 This study examines how stand age affects ecosystem mass and energy exchange
3 response to seasonal drought in three adjacent Douglas-fir (*Pseudotsuga menziesii*
4 (Mirb.) Franco) forests. The sites include two early seral stands (ES) (0-15 years old)
5 and an old-growth (OG) (~ 450-500) forest in the Wind River Experiment Forest,
6 Washington, USA. We use eddy covariance flux measurements of carbon dioxide
7 (F_{NEE}), latent energy (λE) and sensible heat (H) to derive evapotranspiration rate (E_T),
8 bowen ratio (β), water use efficiency (WUE), canopy conductance (G_c), the Priestley-
9 Taylor coefficient (α) and a canopy decoupling factor (Ω). The canopy and bulk
10 parameters are examined to see how ecophysiological responses to water stress, including
11 changes in available soil water (θ_r) and vapor pressure deficit (δe) differ among the two
12 forest successional-stages.

13 Despite very different rainfall patterns in 2006 and 2007, we observed distinct
14 successional-stage relationships between E_T , α , and G_c to δe and θ_r during both years.
15 The largest stand differences were (1) higher morning G_c ($> 10 \text{ mm s}^{-1}$) at the OG forest
16 coinciding with higher CO_2 uptake ($F_{NEE} = -9 \text{ to } -6 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$) but a strong negative
17 response in G_c to moderate δe later in the day and a subsequent reduction in E_T , and (2)
18 higher E_T at the ES stands because midday canopy conductance did not decrease until
19 very low water availability levels ($< 30\%$) were reached at the end of the summer. Our
20 results suggest that early seral stands are more likely than mature forests to experience
21 declines in production if the summer drought becomes longer or intensifies because water
22 conserving ecophysiological responses were only observed at the very end of the seasonal
23 drought period in the youngest stands.

1 **1. Introduction**

2 The landscape of the Pacific Northwest, USA is dominated by tall, long-lived
3 evergreen conifer species that are well adapted to a distinct seasonal climate. This
4 climate regime includes a cool and wet season, and a warm and dry season which are
5 determined by the locations of the Aleutian low during the wet winter months and the
6 Pacific high during the dry summer. Climate change scenarios currently predict that
7 while the Pacific Northwest region will likely receive more precipitation during the
8 winter than it does now, the summers are expected to be warmer and drier creating
9 ecophysiological stress on forest communities and species (Mote et al. 2005). Some
10 ecologists believe that a more intense summer drought will generally have a greater
11 impact on Pacific Northwest tree species, including the dominant low-elevation species
12 Douglas-fir (*Pseudotsuga menziesii* var *menziesii* (Mirb.) Franco) and western hemlock
13 (*Tsuga heterophylla* (Raf.) Sarg.) than the expected annual temperature increases (Mote
14 et al. 2003). Enhanced water stress is a particular concern for the regeneration of
15 Douglas-fir forest stands on harvested lands in the Western Cascade Mountains, which
16 can make up to 40% of the landscape coverage (Cohen et al. 1996). Mature trees in
17 intact, closed stands are likely partially buffered from increased drought stress (Waring
18 and Franklin 1979) but early seral stands (< 15 years old) may have trouble surviving
19 prolonged, extremely dry summers.

20 In Douglas fir forests stomatal conductance and net photosynthesis are strongly
21 dependent on the canopy's microclimate and decline throughout the course of the drought
22 season as vapor pressure deficit (δe) increases and soil water content (θ_v) decreases (e.g.,
23 Waring and Franklin 1979, Winner et al. 2004, Falk et al. 2008) although stand age

1 certainly affects this response. Stomatal control is the main cause for variation in the
2 surface energy budget of forests (Stewart 1988) because stomatal aperture controls how
3 available energy is partitioned between sensible heat and latent heat (or transpiration).
4 Partial stomatal closure restricts water vapor exchange between the leaf and atmosphere
5 and consequently increases leaf temperature and sensible heat transfer. Douglas-fir and
6 western hemlock foliage have the ability to induce stomatal closure and conserve water in
7 the short-term by limiting transpiration but this occurs at the expense of reducing the
8 photosynthetic rate, and over the long-term, also reduces tree growth and wood
9 production (Bower et al. 2005).

10 In developing forest stands, productivity is closely dependent on available soil
11 water because (1) soil moisture determines the biomass of foliage, and (2) moisture stress
12 affects the photosynthetic efficiency of that foliage (Kimmins 1987). Prior experiments
13 give us an idea for how evergreen needleleaf trees in southern Washington survive the
14 annual, five-month drought event. Site water availability and tree water use and demand
15 measurements have been taken in a 20-year old Douglas-fir and the 450-year old
16 Douglas-fir/western hemlock forest in the Wind River Experimental Forest, Washington.
17 Warren et al. (2005) showed that soil moisture in the shallow 0.15-0.60 m soil layer
18 declined by 40-45% during the summer drought period while deep soil (2 m) released
19 only 5% of its original volume. The importance of hydraulic redistribution (HR) at these
20 forest sites, whereby roots are able to lift water from deeper, moist soil horizons and
21 release it into shallower, drier soil portions is reinforced by the work of Domec et al.
22 (2004). Their data showed that HR at the highest rates replenished 60% of the previous
23 day's water use and was critical for maintaining shallow root function and preventing

1 total stomatal closure during drought conditions in the Douglas-fir stands. Brooks et al.
2 (2002) further found that the effects of summer drought in the 20 year-old Douglas-fir
3 forest were partially muted by HR which accounted for an additional 16 days of stored
4 water to remain in the upper soil horizons after a 60-day drought. But HR is not expected
5 to be a significant process in this study's early seral stands because 0-15 year-old trees
6 are likely to lack the necessary root system to reach the deeper water reserves during the
7 dry summer months.

8 Although experiments have shown that mature stands have access to deep water
9 reserves during drought periods, foliage at the top of very tall trees often exist near
10 critical values for cavitation, a condition largely set by the distance between the water
11 table and the hydraulic capacity of the xylem (Ryan and Yoder 1997, Ryan et al. 2006).
12 High hydraulic path-length resistance may decrease productivity in taller, older trees
13 because stomata in tall trees are more often closed than in younger, shorter trees and
14 consequently carbon gain is reduced during the midday hours (see "hydraulic limitation
15 hypothesis", Ryan and Yoder 1997). Several branch-level, gas exchange studies have
16 shown that stomatal conductance decreases with increasing tree age and height (Yoder et
17 al. 1994, Ryan et al. 2000), while other studies have shown that stomatal conductance
18 measurements fail to conclusively support the hydraulic limitation to gas exchange
19 hypothesis (Bauerle et al. 1999, Phillips et al. 2002, McDowell et al. 2005). Identifying
20 any universal age-effect responses in Douglas-fir stands from these types of studies needs
21 to be done with caution because the branch-level data are scaled up to the stand level
22 based on short measurement periods and small sampling sizes (e.g., Raulier et al. 2000).

Our study instead uses the eddy covariance (EC) technique which makes measurements of microclimate, mass and energy fluxes between the whole forest ecosystem and the atmosphere. We collected ecosystem-level data over two growing seasons (May through October 2006, 2007) at the Wind River old-growth forest and at Early Seral North in 2006 and Early Seral South in 2007. All of our study sites were dominated or co-dominated by Douglas-fir, an extremely long-lived (up to ~700 years) pioneering species and the three stands are representative of the youngest and oldest Douglas-fir successional stages. Our objectives were to: (1) assess how summer-time reductions in soil moisture availability and increases in vapor pressure deficit influence ecosystem-atmospheric carbon dioxide (F_{NEE}), evapotranspiration rate (E_T) and energy exchange in two distinct forest age classes, and (2) compare site ecophysiological responses (e.g., canopy conductance, Priestley-Taylor coefficient, canopy decoupling factor) to microclimate conditions during the seasonal drought period.

2. Materials and Methods

Site Description

Old-growth canopy

The old-growth forest is in the Thorton T. Munger Research Natural Area (RNA) (45° 49' 13.76" N, 121° 57' 06.88" W; 371 m a.s.l.), a preserved 478 ha. section of the Wind River Experimental Forest in the Gifford Pinchot National Forest, Washington, USA. The stand is dominated by Douglas-fir (mean height = 52 m, maximum height = 65 m), the colonizing tree species, and western hemlock (mean height = 19 m, max height = 55 m), a shade tolerant, climax species (Ishii et al. 2000). Other tree species found in the T.T. Munger RNA include the conifers: western red cedar (*Thuja plicata* Donn.), noble fir (*Abies procera* Rehd.), grand fir (*Abies grandis* (Dougl.) Forbes), western white pine (*Pinus monticola* Dougl.), Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) and pacific yew (*Taxus brevifolia* Nutt.), and the angiosperms: cascara buckthorn (*Rhamnus purshiana* (DC.) Cooper), Pacific dogwood (*Cornus nuttallii* (Aud.) Torr.) and red alder (*Alnus rubra* Bong.). Ground species include salal (*Gaultheria shallon* Pursh), vine maple (*Acer circinatum* Pursh), Oregon-grape (*Berberis nervosa* Pursh), vanillaleaf (*Achlys triphylla* (Smith) DC.), bracken fern (*Pteridium aquilinum* (L.) Kuhn), sword fern (*Polystichum munitum* (Kaulf.) C. Presl) and deer fern (*Blechnum spicant* (L.) Roth) (Franklin 1972, DeBell and Franklin 1987, Harmon et al. 2004).

The vertical canopy is structurally complex due to a mixture of tree ages (0 to ~500 years old) amongst shade-tolerant and shade-intolerant species. Strong vertical temperature and humidity gradients are periodically present (Paw U et al. 2004, Pyles et al. 2004, Falk et al. 2005) and are indicative of reduced aerodynamic mixing conditions

throughout the canopy and increased boundary-layer resistance around the foliage. Overhead canopy gap fraction is 0.52 (Parker et al. 2002) and leaf area index (LAI) measurements range from 8.2 to 9.2 m² m⁻² (Thomas and Winner 2000, Parker et al. 2004) and are divided unevenly between the middle and upper canopy (4.8 m² m⁻²), lower canopy (2.1 m² m⁻²) and understory (1.7 m² m⁻²). Western hemlock and western red cedar represent more than half of the stand LAI but Douglas-fir foliage dominate the upper canopy (Thomas and Winner 2000), the driest and brightest microenvironment, and have disproportionate control over ecosystem mass and energy exchange, including transpiration (Winner et al. 2004). Deciduous vegetation are a relatively insignificant component (maximum coverage < 15%) of stand LAI.

Early seral canopies

The Early Seral North (ESN) (45°49'37.2" N, 121°57'39.6" W; 361 m a.s.l.) is a re-established evergreen needleleaf forest on a 7 hectare clear-cut patch, 1.25 km northwest of the canopy crane. This stand represents a third generation Douglas-fir ecosystem: the original old-growth forest was logged in 1920 and a clear-cut harvest was done in 1994 on the 80-year old Douglas-fir trees. In 1997, the stand was seeded with Douglas-fir saplings at 741 tree ha⁻¹. The second most common tree was the deciduous species red alder which was found predominately in the southern portion of the stand. Western hemlock and western white pine seedlings were also present but in insignificant amounts. Douglas fir height and diameter at breast height (d.b.h) measurements were taken in September 2005: mean height = 4.4 m, height range = 1.2 to 5.3 m, and mean d.b.h = 5.7 cm. Digital hemispheric photography (DHP) estimates of canopy LAI were

1 1.5 m² m⁻² (excluding ground species) for the month of August 2006. LAI measurements
2 of the herbaceous/understory species were not taken. Ground cover species were diverse
3 in the summer months and included salal, Oregon-grape, bracken fern, sword fern and
4 blackberry (*Rubus ursinus* Cham. & Schltdl.).

5 The Early Seral South (ESS) stand (45°48'47.4" N, 121°57'32.9" W; 371 m a.s.l.)
6 is an abandoned clear-cut (1990), 1.1 km southwest of the canopy crane and was
7 naturally established with Douglas-fir from surrounding cone crops. In July 2007 the
8 average Douglas-fir tree height was 3.58 ± 0.84 m and d.b.h was 4.47 ± 1.6 cm (n = 95
9 trees). The estimated tree density was 1063 trees/hectare (biomass survey included 8
10 plots of 100 m² each). This was the most open stand of the three and canopy LAI was 0.9
11 m² m⁻² (DHP taken in August 2007). Tree cores showed that stand-representative
12 Douglas-fir trees were between 9 and 12 years of age in 2007 (n = 10 trees). Other tree
13 species included western white pine, red alder and planted Pacific silver fir and pacific
14 yew seedlings, each in insignificant amounts. Bracken fern was the dominant ground
15 species from May until September. In August, aboveground fern weight (dried) was 140
16 g m⁻² and DHP-estimated fern LAI was 0.4 to 0.5 m² m⁻². Grasses and scotch broom
17 bushes (*Cytisus scoparius* (L.) Link) were also common in the more open areas.

18
19 *Belowground description*

20 Coarse roots of mature Douglas-fir extend 1-2 m deep although most root biomass
21 in the old-growth stand is concentrated within the first 0.5 m of the soil profiles (Shaw et
22 al. 2004). At the early seral stands coarse roots were observed down to 0.5 m and fine
23 roots were primarily in the 0 to 0.3 m soil layer. Area soils are medial, mesic, Entic

Vitrands and are 2-3 m deep, well drained, and derived from volcanic material (Shaw et al. 2004). These soils are classified as silt loams and are generally stone-free, high in organic material and relatively nitrogen deficit in the root zone at the Wind River sites. Stand-specific soil properties are listed in Table 1. The water table depth is both spatially and temporally heterogeneous at the old-growth forest and ranges from 0.3-0.5 m in the winter months to 2.0-2.4 m in the dry summer months (Shaw et al. 2004). Water table depth was not measured at the early seral stands but is assumed to be within the range found at the old-growth forest. Field capacity (θ_v at matrix potential = - 10 kPa) for this soil type is $0.30 \text{ m}^3 \text{ m}^{-3}$ or 30%, permanent wilting point (θ_v at matrix potential = - 1500 kPa) is $0.14 \text{ m}^3 \text{ m}^{-3}$ or 14%, and available soil water content to the plants ($\theta_v = \theta_{v-10 \text{ kPa}} - \theta_{v-1500 \text{ kPa}}$) is $0.16 \text{ m}^3 \text{ m}^{-3}$ or 16%. For root zones of 1.5 m and 0.6 m, respectively at the old-growth forest and early seral stands, maximum available water storage was estimated to be 240 mm (OG) and 96 mm (ES).

Instrumentation and Flux Calculations

Old-growth forest

Ecosystem carbon dioxide, water vapor and energy fluxes were measured using eddy covariance methodology (see for example Wofsy et al. 1993, Hollinger et al. 1994, Goulden et al. 1996, Paw U et al. 2000, Baldocchi 2003). The EC system consisted of a sonic anemometer (Solent HS, Gill Instruments, Lymington, England, UK) and a closed-path infrared gas analyzer (IRGA) (LI-7000, LI-COR Inc., Lincoln, Nebraska, USA), which measured the wind velocity vectors and air temperature, and concentrations (mixing ratios) of water vapor (H_2O) and carbon dioxide (CO_2), respectively, at 10 Hz.

The IRGA and sonic anemometer were mounted on a horizontal boom at a height of 67 meters off the canopy crane so that the anemometer faced west, the predominant wind direction and direction of greatest homogenous fetch (> 1 km). Carbon dioxide (F_{CO_2} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), sensible heat (H , W m^{-2}) and latent energy (λE , W m^{-2}) fluxes were computed with FORTRAN90 code using a 30-minute averaging period and a horizontal coordinate rotation. The rate of change in CO_2 concentration (storage flux, S_{CO_2} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) within the canopy volume was estimated using 30-minute changes in the mean CO_2 mixing ratio measured at the top of the canopy (Falk et al. 2008). To account for any CO_2 stored within the canopy and below the detection height of the instruments, S_{CO_2} was added to F_{CO_2} to estimate net ecosystem exchange of carbon (F_{NEE} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) on a half-hourly basis. Half-hour measurements of F_{NEE} and λE were further screened for outliers and gap-filled (16% of data in 2006 and 11% in 2007) using a running-mean and look-up table approach (Reichstein et al. 2005). We report no nighttime flux data in this study except in the daily evapotranspiration sums. For further details on the EC post-processing see Paw U et al. (2004) and Falk (2005).

Meteorological instrumentation at the canopy crane included air temperature/relative humidity (sheltered HMP-35C, Vaisala Oyj, Helsinki, Finland) and incident photosynthetically active radiation sensors (PAR) (190-SB, LI-COR Inc.) mounted at heights of 2 (below canopy measurement) and 70 (above canopy measurement) meters along the crane tower, and a 4-stream (up-welling and down-welling short- and long-wave radiation) net radiometer (CNR 1, Kipp and Zonen, Delft, The Netherlands) was mounted at a height of 85 m. Additionally, soil temperature was measured at depths of 0.05, 0.10 and 0.15 m (CS106B, Campbell Scientific Inc.).

Ground heat flux was measured with a HFT-3.1 soil heat flux plate (Radiation and Energy Systems (REBS), Seattle, Washington, USA) buried 0.075 m below the surface. The meteorological measurements were collected as 30-minute averages and were logged continuously from May 2006 through October 2007.

Early Seral North and South

10 Hz measurements of horizontal (u and v) and vertical (w) wind velocity and air temperature were made with a CSAT-3 sonic anemometer (Campbell Scientific Inc., Logan, Utah, USA), and densities of CO₂ and H₂O vapor were measured with an open-path fast response IRGA (LI-7500, LI-COR Inc.). F_{CO_2} , λE , and H were calculated in real-time using a 30-minute averaging period with the CR1000 eddy covariance program (Campbell Scientific Inc.). F_{CO_2} and λE were also corrected for any measurement errors associated with density fluctuations (Webb et al. 1980, known as WPL80 corrections). During post-processing, all scalar and energy fluxes were re-calculated after the mean cross-wind (\bar{v}) and vertical wind (\bar{w}) velocities were rotated to zero (following the natural wind coordinate system). The rate of change of CO₂ concentration (S_{CO_2}) within the canopy was estimated using the half-hourly changes in the CO₂ mixing ratio measured at the top of the canopy and was added to F_{CO_2} to estimate F_{NEE} . Half-hour scalar and energy fluxes were quality controlled for non-preferred wind directions, inadequate fetch (using a parameterized footprint model, Kljun et al. 2004), low turbulence conditions (determined by a ratio of mean wind velocity to a turbulent energy velocity scale), heavy precipitation events, and times of general instrument failure.

1 Missing or excluded scalar and energy fluxes were gap-filled using a running-mean
2 approach (Reichstein et al. 2005).

3 At ESN, the sonic anemometer was mounted facing west-southwest with a fetch
4 of 210 m over homogeneous Douglas-fir trees. Both the LI-7500 and CSAT-3 were
5 mounted at 5.5 m a.g.l., 1.1 m above the ESN canopy, on a boom extending from a 6 m
6 tall tower. Tower-based micrometeorological data included half-hour measurements of
7 air temperature/relative humidity (sheltered HMP-35C, Vaisala Oyj), net radiation (Q7.1,
8 REBS) and soil temperature (0.05, 0.10 and 0.15 m) (CS106B, Campbell Scientific Inc.).
9 Ground heat storage was calculated from the soil temperature profiles. Fluxes and
10 micrometeorological data were collected at ESN from May through October, 2006. The
11 instrument setup at ESS was identical except that the LI-7500 and CSAT-3 were mounted
12 at 5 m a.g.l., 1.4 m above the canopy facing south (170°), and up- and down-welling PAR
13 sensors (190-SB, LI-COR Inc.) were added at the top of the tower at a height of 6 m a.g.l.
14 EC data at ESS were collected May through August 2007 (EC fluxes end in August due
15 to instrument failure) and meteorological data from May through October 2007.

16 A simple, parameterized footprint model (Kljun et al. 2004,
17 <http://footprint.kljun.net/index.php>) was used to determine the extent of which measured
18 turbulent fluxes were influenced by scalar sources outside of the early seral stands. The
19 model showed that daytime (10:00 – 14:00) footprint estimates range from 75 m (east
20 upwind direction) to 100 m (north upwind direction) at ESN and 77 m (east upwind
21 direction) to 115 m (north upwind direction) at ESS, translating into fetch-to-EC
22 instrument height ratios of 14:1 to 23:1. Available (i.e., homogeneous vegetation) fetch-
23 to-EC instrument height ratios averaged 33:1 and 34:1 at ESN and ESS, respectively, but

1 ranged from 10:1 to 44:1 depending on wind direction. Half-hour fluxes taken under
2 inadequate fetch conditions (i.e., when the modeled footprints estimated that scalar
3 sources originated from outside the clear-cut boundaries) were removed from the data
4 series, as well as wind directions at Early Seral North where red alder made up a
5 significant portion of the flux footprint.

6 7 **Water supply and demand measurements**

8 Direct measurements of canopy water availability included precipitation and
9 volumetric soil moisture. Precipitation (P , mm day⁻¹) was measured at the Carson Fish
10 Hatchery NOAA Station (45°31'12" N, 121°34'48" W; 345.6 m a.s.l.) using a rain and
11 snow gauge (385 heated, Met One Instruments, Inc., Grants Pass, Oregon, USA). The
12 NOAA station is located 5 km north of the canopy crane in the Wind River Valley at a
13 similar elevation. Soil water content (θ_v , m³ m⁻³) at the old-growth forest was measured
14 over an integrated depth of 0 to 0.30 m (3 replicates) in 2006 with a time-domain
15 reflectometry (TDR) system (TDR100, Campbell Scientific Inc.) and in staggered depths
16 down to 2 m in 2007 with Sentek soil moisture probes (4 replicates) (Sentek
17 EnviroSMART, Sentek Sensor Technologies, Stepney, Australia). At ESN, θ_v was
18 measured with the TDR100 system over integrated depths of 0 to 0.30 and 0.30 to 0.60 m
19 (2 replicates). The TDR100 system was moved to ESS in 2007 where θ_v was measured
20 over integrated depths of 0 to 0.30, 0.30 to 0.60 and 0.60 to 0.90 m (2 replicates). Our
21 study reports soil moisture measurements in relative volumetric soil water (θ_r), where $\theta_r =$
22 $(\theta_v - \theta_{v-1500 \text{ kPa}})/(\theta_{v-10 \text{ kPa}} - \theta_{v-1500 \text{ kPa}})$. θ_r is a dimensionless number that ranges from 0 to 1
23 and represents the fraction of available soil water in the root zone.

Water vapor loss from the canopy was estimated using the 30-minute averaged λE to calculate evapotranspiration rate (E_T , mm half hour⁻¹), and summed over daily and monthly intervals. Equilibrium evapotranspiration rate (E_{Teq} , mm half hour⁻¹) was calculated based on the energy-balance technique ($\lambda E + H = R_n - S$, where S = energy storage flux) and a modification of the Penman equation (Penman 1948) following Denmead and McIlroy (1970),

$$E_{Teq} = \left(\frac{\Delta}{\Delta + \gamma} \right) (R_n - S_g) \quad (1)$$

In Eqn. 1, Δ is the slope of the saturation vapor pressure curve (kPa K⁻¹), γ is the psychrometric constant (kPa K⁻¹), R_n is net radiation (W m⁻²) and S_g is the ground heat storage flux (W m⁻²). Equilibrium E_T is a measure of the climatologically expected evapotranspiration over a moist surface based only on temperature and available energy. The Priestley-Taylor coefficient, α , the ratio of measured E_T to equilibrium E_T , was calculated using Eqn. 2 (Priestley and Taylor 1972),

$$\alpha = \frac{E_T}{E_{Teq}} \quad (2)$$

The ratio of measured E_T to equilibrium E_T is site-dependent and varies with surface vegetation (Denmead 1969) and microclimate conditions, including soil water availability (Slatyer and Denmead 1964, Priestley and Taylor 1972, Black 1979). Eqn. 2 gives a maximum α value of one assuming that there is no upwind advection of heat added to the system (e.g., an “oasis effect”). Magnitudes of α approach one as E_T approaches E_{Teq} and measured evapotranspiration is largely controlled by aerodynamic resistance ($R_a = \frac{1}{G_a}$) and the subsequent water vapor gradient between the canopy

1 surface and atmosphere, than by canopy resistance ($R_c = \frac{1}{G_c}$) to water vapor transfer. As
 2 α approaches zero, the measured evapotranspiration rate is less than the expected, energy-
 3 limited rate (E_{Teq}) and ecosystem water loss is strongly controlled by canopy resistance
 4 (i.e., degree of stomatal closure) to surface-atmospheric water exchange.

5

6 **Bulk canopy and mechanistic measurements**

7 Bulk canopy and mechanistic variables including water use efficiency, canopy
 8 conductance and a canopy decoupling factor were calculated for daytime (down-welling
 9 shortwave radiation $> 10 \text{ W m}^{-2}$) half-hour periods only. Water use efficiency (WUE) is
 10 defined as the total mass of dry matter produced by photosynthesis for every kilogram of
 11 water lost by vegetation through transpiration (e.g., Rosenberg et al. 1983). Here we
 12 defined a midday WUE as the ratio of F_{NEE} ($\text{g C m}^{-2} \text{ half hour}^{-1}$) to E_T ($\text{kg H}_2\text{O m}^{-2} \text{ half}$
 13 hour^{-1}), averaged between the hours of 10:00 and 15:00 when λE was greater than zero
 14 (following Berbigier et al. 2001). Following Stewart (1988), canopy conductance (G_c)
 15 was estimated using the inverted Penman-Monteith equation (Monteith 1964):

$$16 \quad G_c = \left[\frac{\rho c_p \delta e}{\gamma \lambda E} + \frac{\frac{\Delta}{\gamma} \beta - 1}{G_a} \right]^{-1} \quad (3)$$

17 In Eqn. 3, G_c is canopy conductance (m s^{-1}), ρ is air density (kg m^{-3}), c_p is specific
 18 heat ($\text{J kg}^{-1} \text{ K}^{-1}$), δe is vapor pressure deficit (kPa), λE is latent energy (W m^{-2}), β is the
 19 bowen ratio ($\frac{H}{\lambda E}$), and G_a is aerodynamic conductance for momentum transfer ($G_a =$

20 $\frac{u_*^2}{U}$, m s^{-1} , where u_* is friction velocity, m s^{-1} , and U is mean wind speed, m s^{-1}). Eqn. 3

1 includes both a canopy conductance-driven component (first term, right hand side of Eqn.
2 3) and a radiation-driven component (second term, RHS of Eqn. 3) so that the proportion
3 of E_T controlled by the two drivers can be represented by a canopy decoupling factor, Ω
4 (Jarvis and McNaughton 1986), Eqn 4:

$$\Omega = \frac{\frac{\Delta}{\gamma} + 1}{\frac{\Delta}{\gamma} + 1 + \frac{G_a}{G_c}} \quad (4)$$

6 Ω is a dimensionless number that ranges from 0 to 1 depending on whether E_T is
7 controlled strongly by G_c and δe (Ω approaches zero) and is an aerodynamic driven
8 process, or whether E_T is determined by the amount of available energy ($R_n - S$) to the
9 canopy (Ω approaches 1). If a canopy is completely dry at the surface and one assumes
10 that E_T is approximately equal to the transpiration flux, then Ω refers to the degree to
11 which transpiration is uncoupled to atmospheric δe . In a forest canopy where surface
12 roughness is high, Ω is mostly dependent on wind speed, and gas exchange will be
13 strongly coupled to atmospheric saturation conditions ($\Omega < 0.2$). As soil moisture
14 decreases, Ω also decreases and canopy-air coupling is enhanced (Jarvis and
15 McNaughton 1986).

3. Results

Climate and Stand Microenvironments

Water-year precipitation was 2361 mm from October 2005 through September 2006 and 2129 mm in 2006-2007. Although the water-year totals were relatively equal, the timing of precipitation varied amongst years. May through June was wetter (112 mm) in 2006 than in 2007 (64 mm), while July and August were dramatically wetter in 2007 (34 mm) than in 2006 (2 mm). Overall, 2006 had a wetter spring which led into a very dry summer season, while 2007 received less rain in the spring but experienced periodic rain events throughout the summer (Table 2).

Above canopy air temperatures were warmer ($T_{a_{max}}$ was 1 to 2 °C higher) on most summer days at the early seral stands than at the dense old-growth forest. The old-growth forest (2006 and 2007) and ESN canopies were generally cooler than the local air temperature (CFH NOAA meteorological station data), while cooler conditions were not measured at Early Seral South. Larger site temperature differences were observed in the soil temperature measurements. At ESS, the daily maximum soil temperature (0.05 m) was often 10 °C higher than at OG on 2007 sunny summer days. Maximum daily δe was also higher at the early seral stands than at the old-growth forest. June through August mean daily maximum δe was 2.6 kPa at ESN and 1.9 kPa at OG (2006), and 2.4 kPa at ESS and 1.8 kPa at OG (2007) (Table 2).

Relative available soil water content also varied among stands and years although the seasonal drought pattern remained a dominant feature. In 2006, near-surface (0-0.30 m) θ_r equaled one at both ESN and OG during the spring months and began declining between June and July. Relative water availability dropped to a minimum of 0.27 in

1 August at ESN and to 0.26 in September at OG (Table 2). During the 2007 summer
2 months, near-surface θ_r did not reach these low levels. θ_r dropped to a weekly minimum
3 value of 0.67 at ESS in September and 0.52 at OG in August. While the near-surface
4 water availability was less at the old-growth stand than at the early seral stand, the 0.9 to
5 2 m depth θ_v measurements in 2007 revealed that deeper soil layers were not water
6 deficient ($\theta_r = 1$) at OG. At ESS, the deepest θ_v measurements (0.6 to 0.9 m) showed that
7 relative water availability was not significantly higher in this soil layer and available
8 water content was nearly identical to the near-surface measurements from July through
9 September.

11 **Diurnal and Monthly Fluxes**

12 Net radiation was higher at the old-growth stand than at either early seral stand
13 during the months of May through August. Monthly R_n averaged $470 \text{ MJ m}^{-2} \text{ mo}^{-1}$ in
14 2006 and $468 \text{ MJ m}^{-2} \text{ mo}^{-1}$ in 2007 at OG, and $410 \text{ MJ m}^{-2} \text{ mo}^{-1}$ at ESN and 393 MJ m^{-2}
15 mo^{-1} at ESS (Tables 3 and 4). During the summer months at the old-growth stand a
16 greater amount of available energy was on average partitioned into sensible heat (average
17 daily maximum = 350 W m^{-2}) than latent heat (average daily maximum = 200 W m^{-2}).
18 The May-August bowen ratios at OG were higher than those observed at either early seral
19 stand and ranged from 2.05 (June) to 2.61 (July) in 2006 and 1.94 (June) to 2.58 (May) in
20 2007. Peak daytime latent heat fluxes were relatively constant at the old-growth stand
21 from May through August with the exception of a midday λE decline in July 2006. A
22 more distinct λE pattern was observed at the early seral stands with peak λE occurring in
23 June and July (Figures 1b and 2b). July E_T in 2006 was nearly twice as great at ESN

(103 mm mo⁻¹) than at OG (53 mm mo⁻¹) (Table 3), while a smaller increase over 2007 old-growth E_T was also measured at ESS (Table 4).

During May, midday CO₂ fluxes were more than twice as great at the old-growth stand as at either early seral stand (Figures 1c and 2c). Midday net CO₂ uptake at the old-growth stand peaked in June and declined throughout the latter summer months at OG. At the early seral stands, the greatest differences in midday CO₂ fluxes occurred between the months of May and June. Mean midday F_{NEE} increased from -3.2 to -9.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at Early Seral North and from -4.6 to -8.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at Early Seral South during this period. A lag of ~ 2 hr occurred in the timing between daily peak flux exchange at ESS and OG in 2007 but not at ESN and OG in 2006. This time lag created a longer period of net CO₂ uptake in May at the old-growth stand but a reduced period of CO₂ uptake at OG during July as compared to Early Seral South (compare boxed regions in Figure 2c). Peak λE at ESS also occurred later in the afternoon than at OG from May through August 2007 resulting in higher total daily E_T at the younger stand.

Ecosystem Response to Water Stress

Precipitation, θv and δe effects on E_T

A ratio of precipitation to evapotranspiration ($\frac{P}{E_T}$) showed that all forest canopies lost more water via evapotranspiration than gained from precipitation during the months of June through August (Tables 3 and 4). Precipitation was assumed equal at all stands so any differences were due only to variations in canopy evapotranspiration. In 2006, we observed very low $\frac{P}{E_T}$ values of just 0.01 at the young stand and 0.02 at the older forest

1 in July and August due to nearly zero precipitation. Early Seral North was likely water
 2 stressed by September 2006 as relative soil moisture fell to 20% in the root zone. Near-
 3 surface θ_r at the old-growth stand was also extremely low although deeper water
 4 measurements were not made that year to accurately determine water availability
 5 throughout the entire root zone. On average the 2007 summer was wetter and larger
 6 stand differences were observed between the old-growth and early seral stands. From
 7 May through August $\frac{P}{E_T}$ was 0.35 (more water limited) at ESS and 0.42 (less water
 8 limited) at OG.

9 A time series of daily maximum δe and daily total E_T at Early Seral South and the
 10 old-growth forest is shown in Figure 3. δe was consistently higher at ESS during the
 11 2007 summer, often by more than 1 kPa (circled data points in Figure 3). In June, higher
 12 δe coincided with increased canopy water loss (1 to 2 kg H₂O m⁻² day⁻¹) at the early seral
 13 stand, while in August, daily E_T was moderate and closer to E_T observed at OG (compare
 14 squared data points in Figure 3) even though δe remained higher at the early seral site.
 15 Figure 4 shows that E_T was not closely related to δe at the old-growth forest ($R^2 = 0.0$)
 16 during the month of June in both 2006 and 2007 while a stronger relationship between E_T
 17 and δe was observed at ESN ($R^2 = 0.47$) and ESS ($R^2 = 0.78$). E_T at the old-growth forest
 18 was more closely linked to vapor pressure deficit in August ($R^2 = 0.6$ in 2006, $R^2 = 0.34$
 19 in 2007) than during early summer. For equivalent daily maximum δe (e.g., 2 kPa) total
 20 daily E_T was smaller in August (1.5 to 2.5 kg H₂O m⁻² day⁻¹) than in June (2.5 to 3.5 kg
 21 H₂O m⁻² day⁻¹) at all forests.

22 Summer α ranged from a low of 0.35 at OG (July) to a high of 0.74 at ESN (July)
 23 in 2006 and from 0.39 (July) at OG to 0.63 (June) at ESS in 2007 (Tables 3 and 4).

Overall, both early seral stands had higher Priestley-Taylor coefficients (~ 0.5 to 0.6) than the old-growth forest (~ 0.4) during the drought seasons. The Priestley-Taylor coefficient (α) increased logarithmically with canopy conductance in all stands (e.g., $R^2 = 0.34$ at ESN) so that measured E_T was closer to equilibrium or the expected E_T at the higher G_c values. The relationship between α and relative available soil water was less straightforward (Figure 5). At the old-growth forest and Early Seral South a correlation between the Priestley-Taylor coefficient and θ_r was not found ($R^2 = 0.0$). At Early Seral North α dropped from an average of 0.73 to 0.55 as θ_r conditions decreased and approached 20% (Figure 5).

Bulk canopy parameter and mechanistic responses

We measured higher WUE at the old-growth stand than at either of the early seral stands. Mean midday WUE during the summer drought was 2.5 ± 1.1 g C / kg H₂O at OG and 1.6 ± 1.0 g C / kg H₂O at ESN in 2006 (Table 3), and 2.2 ± 1.0 g C / kg H₂O at OG and 1.5 ± 0.7 g C / kg H₂O at ESS in 2007 (Table 4). The old-growth stand was slightly more water use efficient in 2006 than in 2007 and consistently more water use efficient than either of the early seral stands. Figure 6 shows average canopy conductance from May through October at the old-growth and early seral stands in 2006 and 2007. Overall, higher values of G_c were observed in 2006 than in 2007 and G_c magnitudes were higher at the beginning of the drought season than at the end. Site differences in diurnal G_c values were also observed. Canopy conductance was higher at the early seral stands during the afternoon hours than at the old-growth forest while morning G_c was often higher at the mature forest. Canopy conductance began declining

earlier in the day at OG suggesting that stomates are shutting down at lower δe levels in the old-growth Douglas-fir/western hemlock forest than in the 4 m tall early seral trees. Figure 7 further details the difference between mean canopy conductance in May and July 2007 at ESS and OG during the hours of 10:00, 13:00 and 16:00. In May, G_c declined at similar rates ($\sim 0.2 \text{ mm s}^{-1}$ per half hour) at both stands and averaged 7.4 mm s^{-1} (OG) and 7.6 mm s^{-1} (ESS) at 10:00, 6.4 mm s^{-1} (OG) and 6.5 mm s^{-1} (ESS) at 13:00, and 4.7 mm s^{-1} (OG) and 4.6 mm s^{-1} (ESS) at 16:00. In contrast, August G_c declined more rapidly at the old-growth stand (0.3 mm s^{-1} per half hour) than at ESS (0.1 mm s^{-1} per half hour) beginning at the noon hour. By early evening, G_c averaged less than 4 mm s^{-1} at OG but remained around 6 mm s^{-1} at ESS.

A close look at canopy conductance in Figure 8 reveals both site and monthly differences in leaf-atmosphere gas exchange response to evaporative demand at ESS and OG. At low δe values ($< 0.5 \text{ kPa}$) the OG stand had higher G_c (> 2 to 3 mm s^{-1}) than the young stands but beyond values of 1 to 1.5 kPa , G_c at OG rapidly declined with increasing δe even though available soil moisture was not low (e.g. $\theta_r < 50\%$) in May and June. In general, G_c was lower in July and August than in May and June at both stands for all vapor pressure deficit levels below 2.5 kPa . Beyond 2.5 kPa , the rate of canopy conductance decline with increasing vapor pressure deficit was strongest at OG. The minimum δe threshold to produce very little response in G_c (i.e., $\frac{\partial G_c}{\partial \delta e}$ approaches zero) was 3 kPa and 4 kPa at ESS in May-June and in July-Aug. The old-growth stand had no observable δe - G_c threshold response in May-June but was 3.5 kPa in July-Aug. Figure 9 illustrates how the δe - G_c responses at OG and ESS differ from the beginning of the drought season to conditions at the end. In May and June 2007, canopy conductance

1 declined sharply at OG from 4 to 1 mm s⁻¹ across the highest δe levels (2 to 3.5 kPa)
2 while ESS G_c dropped only from 5 to 3 mm s⁻¹ (gray triangles in Fig. 9). In contrast in
3 July and August, ESS G_c declined sharply from 4 to 2 mm s⁻¹ across the highest δe levels
4 (3 to 4.5 kPa) while G_c remained level at 2 mm s⁻¹ at the old-growth forest (gray circles in
5 Fig. 9).

6 At very high δe (> 4.5 kPa), canopy conductance was low (approximately 2 mm s⁻¹)
7 in all stands but we found that evapotranspiration was more directly related to available
8 energy than to stomatal control as shown by higher decoupling coefficients (e.g. at ESN,
9 $\Omega = 0.27$ for $\delta e > 4.5$ kPa and $\Omega = 0.14$ for $2.5 < \delta e < 3.5$ kPa). The decoupling
10 coefficients at the old-growth stand in 2006 were on average ($\Omega = 0.18$) equal to those at
11 Early Seral North ($\Omega = 0.18$), while OG Ω values in 2007 were significantly higher ($\Omega =$
12 0.31) than in 2006 and higher than those found at Early Seral South ($\Omega = 0.16$).

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4. Discussion and conclusions

Douglas-fir/western hemlock stands in the Pacific Northwest have adapted to seasonal moisture constraints on photosynthesis by assimilating large amounts of carbon during the wetter and cooler spring months (Waring and Franklin 1979) while during the summer, stomatal closure is induced as vapor pressure gradients between the leaf and atmosphere increase. Our study showed that G_c was notably reduced after the noon hour in mid-summer at the old-growth forest regardless of soil moisture availability. While relative near-surface soil moisture was noticeably lower at the old-growth forest in 2006 ($\theta_r \sim 25\%$) than in 2007 ($\theta_r \sim 55\%$), the mature stand likely had access to deep soil water supplies during both drought seasons because (1) relative soil moisture never dropped below 90% at the 1 m depth when these measurements were available, (2) the root zone extends down to 2 m for the oldest trees, and (3) there is prior evidence of hydraulic redistribution in the soils at this stand (Brooks et al. 2002, Warren et al. 2005). The phenomenon of stomatal closure in mature trees regardless of soil moisture has also been noted by Zweifel et al. (2002) in a 250-year old Norway Spruce stand, whereby they observed midday stomatal closure on most sunny days during permanently wet soil conditions.

Even under moderate δe levels, foliage at the tops of tall evergreen conifers trees often reach near critical values for cavitation due to a long path distance between the water table and the hydraulic capacity of the xylem, and as a result, shut their stomata frequently (Ryan and Yoder 1997). Our observation of a rapid decline in G_c between 0.5 and 1.0 kPa in the older forest is consistent with the findings of Ryan and Yoder (1997) as well as with observations of a diurnal hysteresis in sap flow measurements taken at the

bottom and top of tall Douglas-fir trees at Wind River (Cermak et al. 2007). Taken together these datasets suggest that upper canopy Douglas-fir foliage are driving our observed monthly and diurnal fluxes of mass and energy at the old-growth forest. At the early seral stands, we found that canopy conductance was also inhibited by vapor pressure deficit but not until later in the afternoon hours when the highest δe levels were reached and later in the drought season when relative soil moisture was low. Our overall ES G_c observations (e.g., canopy conductance was 2 to 4 mm s⁻¹ higher at the early seral stands than at the old-growth) agree with branch-level measurements taken by Yoder et al. (1994), whereby they found that stomatal conductance is lower in the Wind River old-growth trees than in younger Douglas-fir stands, and by Fessenden and Ehleringer (2002) whom using $\delta^{13}C$ isotopes found evidence that decreased hydraulic conductance in the 450 year-old stand led to lower stomatal conductance in the mature forest than in the younger, shorter trees. δe was almost always lower at the top of the old-growth forest than over the early seral stands suggesting that the stomates are generally closing at lower δe levels in the older stand.

In addition to our successional-stage research, gas exchange studies comparing a Wind River 20-year old Douglas-fir stand and the old-growth forest were made in 1998 and 1999 by Chen et al. (2002, 2004). In their study, Chen et al. (2002) report higher WUE (1.7 g C / kg H₂O) and bowen ratio (2.9) at a Wind River 20-year old stand than at the old-growth forest (WUE = 1.0 g C / kg H₂O, β = 1.6), while total E_T was greater at OG. In contrast, we found higher β , higher WUE and lower E_T at the old-growth forest than the early seral stands. Lower WUE values have also been measured for the 10-year old Douglas-fir age class by Thomas & Winner (2002), whereby they found that WUE

1 was twice as high at the old-growth forest than at nearby younger trees. We suggest that
2 the conflicting nature of succession-stage results at Wind River are a consequence of a
3 rapidly changing Douglas-fir canopy during the first 0-20 years. It is important to note
4 here that other plant species, particularly bracken fern, were a non-negligible component
5 of ecosystem biomass at the younger stands during the summer months. Our
6 measurements of gas exchange are for the ecosystem as a whole and as such we were not
7 able to determine what contribution secondary species had to ecosystem fluxes.
8 Therefore, we are making the following conclusions based on the successional-stage of
9 Douglas-fir forests and not specifically on tree height or tree age:

10 (1) Total evaporation (and fraction of expected E_T) is higher in early seral stands
11 than the old-growth forest during the summer months as a result of higher soil
12 temperatures, higher air temperatures and higher vapor pressure deficits in the open
13 canopies during the mid-afternoon hours. Available soil moisture limited E_T at the early
14 seral stands but only when θ_r dropped below 30%. Total E_T was limited at the old-
15 growth stand during moderate vapor pressure deficits.

16 (2) Early seral stands are likely to be more susceptible to increased water stress
17 than mature stands if the Pacific Northwest drought season becomes longer or more
18 intense due to the young stand's open canopy and extreme microclimate, limited root
19 system (i.e., lack of access to deeper water), and inability to induce stomatal closure and
20 conserve water under moderate levels of vapor pressure deficit.

21 Our results have impacts beyond our specific forest sites since Pacific Northwest
22 forest productivity during the drought season is strongly coupled with evapotranspiration
23 through stomatal control on water vapor loss. Since forest productivity models are often

1 used to estimate present and future carbon stocks and hydrological processes for this
2 region (see for example, Thornton et al. 2002, Law et al. 2004, Turner et al. 2006), our
3 results show the critical need for using stand-specific, ecophysiological response
4 functions in these models, especially for properly capturing ecosystem-level impacts of
5 drought. We found significant differences in the timing, magnitude and environmental
6 controls of ecosystem exchange between the old-growth and early seral stands, indicating
7 the presence of distinct successional-stage mechanisms between the microenvironments
8 and canopies. Considering that Pacific Northwest forests are characterized by regular
9 silviculture harvest rotations and are predicted to have strong water availability changes
10 in the future from regional climate change, we suggest that more successional-stage
11 studies are needed to properly predict future CO₂, water and energy fluxes in evergreen
12 conifer forests.

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References

- Baldocchi, D.D. 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biol.* 9: 479-492.
- Bauerle, W.L., T.M. Hinckley, J. Cermak, J. Kucera and K. Bible. 1999. The canopy water relations of old-growth Douglas-fir trees. *Trees* 13:211-217.
- Berbigier, P., J.M. Bonnefond and P. Mellmann. 2001. CO₂ and water vapour fluxes for 2 years above Euroflux forest site. *Agric. For. Meteorol.* 108:183-197.
- Black, T.A. 1979. Evapotranspiration for Douglas-fir stands exposed to soil water deficits. *Water Resour. Res.* 15:164-170.
- Bower, A.D., W.T. Adams, D. Birkes and D. Nalle. 2005. Response of annual growth ring components to soil moisture deficit in young, plantation-grown Douglas-fir in coastal British Columbia. *Can. J For. Res.* 35:2491-2499.
- Brooks, J.R., F.C. Meinzer, R. Coulombe and J. Gregg. 2002. Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiol.* 22:1107-1117.

- 1 Cermak, J., J. Kucera, W.L. Bauerle, N. Phillips and T.M. Hinckley. 2007. Tree water
2 storage and its diurnal dynamics related to sap flow and changes in stem volume
3 in old-growth Douglas-fir trees. *Tree Physiol.* 27:181-198.
4
- 5 Chen, J.-Q., M. Falk, E. Euskirchen, et al. 2002. Biophysical controls on carbon flows in
6 three successional Douglas-fir stands based on eddy-covariance measurements.
7 *Tree Physiol.* 22:169-177.
8
- 9 Chen, J.-Q., K.T. Paw U, S.L. Ustin, T.H. Suchanek, B.J. Bond, K.D. Brosofske and M.
10 Falk. 2004. Net ecosystem exchanges of carbon, water and energy in young and
11 old-growth Douglas-fir forests. *Ecosystems* 7:534-544.
12
- 13 Cohen, W.B., M.E. Harmon, D.O. Wallin and M. Fiorella. 1996. Two decades of carbon
14 flux from forests of the Pacific Northwest. *Bioscience* 46:836-844.
15
- 16 DeBell, D.S. and J.F. Franklin. 1987. Old-growth Douglas-fir and western hemlock: a
17 36-year record of growth and mortality. *West. J. Appl. For.* 2:111-114.
18
- 19 Denmead, O.T. 1969. Comparative micrometeorology of a wheat field and a forest of
20 *Pinus radiata*. *Agric. Meteorol.* 6:357-371.
21
- 22 Denmead, O.T. and I.C. McIlroy. 1970. Measurements of non-potential evaporation
23 from wheat. *Agric. Meteorol.* 7:285-302.

- 1 Domec, J.C., J.M. Warren, F.C. Meinzer, J.R. Brooks and R. Coulombe. 2004. Native
2 root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa
3 pine: mitigation by hydraulic redistribution. *Oecologia* 141:7-16.
4
- 5 Falk, M. 2005. Carbon and energy exchange between an old-growth forest and the
6 atmosphere. Ph.D. Diss., University of California, Davis, California: 216 pp.
7
- 8 Falk, M., K.T. Paw U, S. Wharton and M. Schroeder. 2005. Is soil respiration a major
9 contributor to the carbon budget within a Pacific Northwest old-growth forest?
10 *Agric. For. Meteorol.* 135:269-283.
11
- 12 Falk, M., S. Wharton, M. Schroeder, S. Ustin and K.T. Paw U. 2008. Flux partitioning in
13 an old growth forest: seasonal and interannual dynamics. *Tree Physiol.* 28:509-
14 520.
15
- 16 Fessenden, J.E. and J.R. Ehleringer. 2002. Age-related variations in delta C-13 of
17 ecosystem respiration across a coniferous forest chronosequence in the Pacific
18 Northwest. *Tree Physiol.* 22:159-167.
19
- 20 Franklin, J.F. 1972. Wind River Research Natural Area. *In* Federal Research Natural
21 Areas in Oregon and Washington-A Guidebook for Scientists and Educators.
22 Pacific NW For. And Range Exp. Sta., Portland, OR: WR1-WR8 pp.
23

- 1 Goulden, M.L., J.W. Munger, S.M. Fan, B.C. Daube and S.C. Wofsy. 1996.
2 Measurements of carbon sequestration by long-term eddy covariance: methods
3 and a critical evaluation of accuracy. *Global Change Biol.* 2:169-182.
4
- 5 Harmon, M.E., K. Bible, M.G. Ryan, D.C. Shaw, H. Chen, J. Klopatek and X. Li. 2004.
6 Production, respiration, and overall carbon balance in an old-growth
7 *Pseudotsuga-Tsuga* forest ecosystem. *Ecosystems* 7:498-512.
8
- 9 Hollinger, D.Y., F.M. Kelliher, J.N. Byers, J.E. Hunt, T.M. McSeveny and P.L. Weir.
10 1994. Carbon-dioxide exchange between an undisturbed old-growth temperate
11 forest and the atmosphere. *Ecology* 75:134-150.
12
- 13 Ishii, H., J.H. Reynolds, E.D. Ford and D.C. Shaw. 2000. Height growth and vertical
14 development of an old-growth *Pseudotsuga-Tsuga* forest in southwestern
15 Washington State, U.S.A. *Can. J. For. Res.* 30:17-24.
16
- 17 Jarvis, P.G. and K.G. McNaughton. 1986. Stomatal control of transpiration: scaling up
18 from leaf to region. *Ad. Ecol. Res.* 15:1-49.
19
- 20 Kimmins, J.P. 1987. *Forest Ecology*. Macmillan Publishing Company, New York: 531
21 pp.
22
- 23 Kljun, N., P. Calanca, M.W. Rotach and H.P. Schmid. 2004. A simple parameterization
24 for flux footprint predictions. *Boundary-Layer Meteorol.* 112:503-523.

- 1 Klopatek, J. 2002. Belowground carbon pools and processes in different age stands of
2 Douglas-fir. *Tree Physiol.* 22:197-204.
3
- 4 Klopatek, J., M.J. Barry and D.W. Johnson. 2006. Potential canopy interception of
5 nitrogen in the Pacific Northwest, USA. *For. Ecol. Man.* 234:344-354.
6
- 7 Law, B.E., D. Turner, J. Campbell, O.J. Sun, S. Van Tuyl, W.D. Ritts and W.B. Cohen.
8 2004. Disturbance and climate effects on carbon stocks and fluxes across
9 Western Oregon USA. *Global Change Biol.* 10:1429-1444.
10
- 11 McDowell, N.G., J. Licata and B.J. Bond. 2005. Environmental sensitivity of gas
12 exchange in different-sized trees. *Oecologia* 145:9-20.
13
- 14 Monteith, J.L. 1964. Evaporation and environment. *In* The State and Movement of
15 Water in Living Organisms. 19th Symp. Soc. Experimental Biology, Academic
16 Press, New York: 205 pp.
17
- 18 Mote, P.W., E. Parson, A.F. Hamlet, et al. 2003. Preparing for climatic change: The
19 water, salmon, and forests of the Pacific Northwest. *Clim. Change* 61:45-88.
20
- 21 Mote, P.W., E. Salathe and C. Peacock. 2005. Scenarios of future climate for the Pacific
22 Northwest. Climate Impacts Group Report, University of Washington: 13 pp.
23

- 1 Parker, G.G., M.M. Davis, and S.M. Chapotin. 2002. Canopy light transmittance in
2 Douglas-fir-western-hemlock stands. *Tree Physiol.* 22:147-157.
3
- 4 Parker, G.G., J. Chen, M.E. Harmon, M.A. Lefsky, D.C. Shaw, S.C. Thomas, S.B. Weiss,
5 R. van Pelt and W.E. Winner. 2004. Three-dimensional structure of the old- growth
6 *Pseudotsuga-tsuga* canopy and its implications for radiation balance, microclimate,
7 and gas exchange. *Ecosystems* 7:440-453.
8
- 9 Paw U, K.T., D.D. Baldocchi, T.P. Meyers and K.B. Wilson. 2000. Correction of eddy-
10 covariance measurements incorporating both advective effects and density fluxes.
11 *Boundary-Layer Meteorol.* 91:487-511.
12
- 13 Paw U, K.T., M. Falk, T.H. Suchanek, et al. 2004. Carbon dioxide exchange between an
14 old-growth forest and the atmosphere. *Ecosystems* 7:513-524.
15
- 16 Penman, H.L. 1948. Natural evaporation from open water, bare soil and grass. *Proc. Roy.*
17 *Soc. Lond.* 193:120-145.
18
- 19 Phillips, N., B.J. Bond, N.G. McDowell and M.G. Ryan. 2002. Canopy and hydraulic
20 conductance in young, mature and old Douglas-fir trees. *Tree Physiol.* 22:205-
21 211.
22

- 1 Priestley, C.H.B. and R.J. Taylor. 1972. On the assessment of surface heat flux and
2 evaporation using large-scale parameters. *Mon. Weather Rev.* 100:81-92.
3
- 4 Pyles, R.D., K.T. Paw U and M. Falk. 2004. Directional wind shear within an old-growth
5 temperate rainforest: observations and model results. *Agric. For. Meteorol.* 125:19-
6 31.
7
- 8 Raulier, F., P.Y. Bernier and C.-H. Ung. 2000. Modeling the influence of temperature on
9 monthly gross primary productivity of sugar maple stands. *Tree Physiol.* 20:333-
10 345.
11
- 12 Reichstein, M., E. Falge, D. Baldocchi, et al. 2005. On the separation of net ecosystem
13 exchange into assimilation and ecosystem respiration: review and improved
14 algorithm. *Global Change Biol.* 11:1424-1439.
15
- 16 Ryan, M.G and B.J. Yoder. 1997. Hydraulic limits to tree height and tree growth.
17 *Bioscience* 47:235-242.
18
- 19 Ryan, M.G., B.J. Bond, B.E. Law, et al. 2000. Transpiration and whole-tree
20 conductance in ponderosa pine trees of different heights. *Oecologia* 124:553-
21 560.
22

- 1 Ryan, M.G., N. Phillips and B.J. Bond. 2006. The hydraulic limitation hypothesis
2 revisited. *Plant Cell Environ.* 29:367-381.
3
- 4 Shaw, D.C., J.F. Franklin, K. Bible, J. Klopatek, E. Freeman, S. Greene and G.G. Parker.
5 2004. Ecological setting of the Wind River old-growth forest. *Ecosystems* 7:427-
6 439.
7
- 8 Slatyer, R.O. and O.T. Denmead. 1964. Water movement through the soil-plant-atmosphere
9 system. *In* E.S. Hills (Ed.). *Water Resources Use and Management*. Melbourne
10 University Press, Melbourne: 276-289 pp.
11
- 12 Stewart, J.B. 1988. Modelling surface conductance of pine forests. *Agric. For.*
13 *Meteorol.* 43:19-35.
14
- 15 Thomas, S.C. and W.E. Winner. 2000. Leaf area index of an old-growth Douglas-fir forest
16 estimated from direct structural measurements in the canopy. *Can J. For. Res.*
17 30:1922-1930.
18
- 19 Thomas, S.C. and W.E. Winner. 2002. Photosynthetic differences between saplings and
20 adults trees: an integration of field results by meta-analysis. *Tree Physiol.* 22:
21 117-127.
22
- 23 Thornton, P. E., B.E. Law, H.L. Gholz, et al. 2002. Modeling and measuring the effects of

1 disturbance history and climate on carbon and water budgets in evergreen needleleaf
2 forests. *Agric. For. Meteorol.* 113:185-222.

3

4 Turner, D.P., W.D. Ritts, J.M. Styles, Z. Yang, W.B. Cohen, B.E. Law and P.E. Thornton.
5 2006. A diagnostic carbon flux model to monitor the effects of disturbance and
6 interannual variation in climate on regional NEP. *Tellus* 58:476-490.

7

8 Waring, R.H. and J.F. Franklin. 1979. Evergreen coniferous forests of the Pacific
9 Northwest. *Science* 203:1380-1386.

10

11 Warren, J.M., F.C. Meinzer, J.R. Brooks and J.C. Domec. 2005. Vertical stratification of
12 soil water storage and release dynamics in Pacific Northwest coniferous forests.
13 *Agric. For. Meteorol.* 130:39-58.

14

15 Webb, E.K., G.I. Pearman and R. Leuning. 1980. Correction of flux measurements for
16 density effects due to heat and water-vapour transfer. *Quart. J Roy Meteorol.*
17 *Soc.*106:85-100.

18

19 Winner, W.E., S.C. Thomas, J.A. Berry, et al. 2004. Canopy carbon gain and water use:
20 analysis of old-growth conifers in the Pacific Northwest. *Ecosystems* 7:482-497.

21

22 Wofsy, S., M.L. Goulden, J.W. Munger, et al. 1993. Net exchange of CO₂ in a
23 midlatitude forest. *Science* 260:1314-1317.

1

2 Yoder, B.J., M.G. Ryan, R.H. Waring, A.W. Schoettle and M.R. Kaufmann. 1994.

3 Evidence of reduced photosynthetic rates in old trees. Forest Science 40:513-

4 527.

5

6 Zweifel, R., J.P. Böhm and R. Häsler. 2002. Midday stomatal closure in Norway spruce-

7 reactions in the upper and lower crown. Tree Physiol. 22:1125-1136.

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1 Tables

	Early Seral North	Early Seral South	Old-Growth Stand
Measurement period			
2006	May - October		May - October
2007		May - August (flux data); May - October (meteorological data)	May - October
Stand properties			
Stand area (ha)	7	10	478
Site Preparation	minimal: post-harvest coarse woody debris (CWD) piles, snags, logs; no fertilization	extensive: no CWD; mechanically homogenized soil to 1 m; no fertilization	none: natural fire recovery
Maximum tree age	10	14	~ 450-500
Mean tree height (m)	4.4	3.6	52 (Douglas-fir) 19 (western hemlock)
Stand density (trees ha ⁻¹)	741*	1063	427 (Shaw et al. 2004)
LAI (m ² m ⁻²)	1.1 – 1.8	0.6 – 1.1	8.2 – 9.2 (Parker et al. 2002)
Foliar C:N	44:1 ± 3	37:1 ± 3	41:1 (Klopatek et al. 2006)
Soil properties			
0-0.15 m			
sand: silt: clay	66:28:6	60:32:8	60:30:10 (Shaw et al. 2004)
C:N	27:1 ± 6	26:1 ± 3	28:1 ± 1 (Klopatek 2002)
Organic C	3.4	2.2	5 – 10% (Shaw et al. 2004)
bulk density (g cm ⁻³)	0.94	1.07	0.83
0.15-0.30 m			
sand: silt: clay	68:26:6	62:29:9	60:31:9 (Shaw et al. 2004)
C:N	28:1 ± 5	26:1 ± 4	25:1 ± 1 (Klopatek 2002)
Organic C	2.9	3.9	5 – 10% (Shaw et al. 2004)
bulk density (g cm ⁻³)	0.94	1.07	0.83

2 **Table 1. Stand descriptions for the 3 forest sites. * Note that stand density is an**
3 **underestimate at ESN because it only includes planted trees and not naturally**
4 **established trees that are present as well.**

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	Ta _{max} (° C)	Tsoil _{max} (° C)	δe _{max} (kPa)	θ _r	Ta _{max} (° C)	Tsoil _{max} (° C)	δe _{max} (kPa)	θ _r	P (mm)	Ta _{max} (° C)
2006	Early Seral North				Old-Growth				CFH	
May	20.0	--	1.5	1.0	18.6	11.7	1.3	1.0	59.2	19.3
June	25.8	19.6	2.5	1.0	22.0	14.8	1.6	1.0	52.3	23.1
July	27.2	21.6	2.6	0.44	25.6	17.7	2.1	0.63	1.0	28.8
Aug.	27.1	19.9	2.6	0.27	25.3	17.3	2.2	0.28	1.3	27.5
Sept.	24.0	16.7	2.2	0.28	22.4	15.1	1.8	0.26	14.2	24.5
Oct.	15.6	12.3	1.1	0.55	14.6	10.6	0.9	0.51	55.6	16.6
Average	23.3	18.0	2.1	0.59	21.4	14.5	1.7	0.63	183.6	23.3
2007	Early Seral South				Old-Growth				CFH	
May	21.0	22.9	2.2	1.0	18.7	13.0	1.5	1.0	34.3	19.8
June	21.6	24.5	1.9	1.0	19.1	14.4	1.4	0.87	30.0	21.3
July	28.8	30.9	2.9	0.89	26.0	18.8	2.2	0.72	18.8	27.8
Aug.	25.1	27.4	2.3	0.73	22.8	16.9	1.8	0.52	15.5	25.4
Sept.	23.0	22.2	--	0.71	19.0	14.2	1.3	0.56	57.7	21.6
Oct.	15.1	11.3	--	1.0	11.6	9.7	0.5	0.94	223.5	12.1
Average	22.4	23.2	2.3	0.88	19.5	14.5	1.5	0.78	379.8	21.3

Table 2. Monthly micrometeorological data at the tower sites and total precipitation and maximum temperature at Carson Fish Hatchery (CFH) NOAA weather station.

2006	Early Seral North							Old-Growth						
	May	June	July	Aug	Sept	Oct	May -Oct	May	June	July	Aug	Sept	Oct	May -Oct
R_n (MJ m ⁻² mo ⁻¹)	302	454	467	417	279	172	350	394	495	525	465	312	202	400
β ($H/\lambda E$)	2.82	0.94	0.78	1.26	1.60	1.30	1.51 \pm 0.35	2.23	2.05	2.61	2.18	1.92	1.46	2.07 \pm 0.45
E_T (mm mo ⁻¹)	49	86	103	68	44	39	388 \pm 17	60	67	53	51	41	31	303 \pm 13
P/E_T	1.22	0.61	0.01	0.02	0.32	1.44	0.60	0.98	0.78	0.02	0.03	0.35	1.78	0.66
α (E_{Teq}/E_T)	0.55	0.69	0.74	0.65	0.52	0.62	0.65	0.42	0.47	0.35	0.43	0.36	0.49	0.42
F_{NEE} (μ mol m ⁻² s ⁻¹)	-3.2	-9.0	-10.2	-8.0	-3.4	-2.2	-6.0 \pm 1.8	-9.3	-11	-9.2	-7.3	-5.8	-6.9	-8.3 \pm 2.0
WUE (g C kg H ₂ O ⁻¹)	2.1	1.6	1.7	1.8	1.2	1.8	1.6 \pm 1.0	2.3	2.1	2.7	2.5	2.2	2.9	2.5 \pm 1.1
G_c (mm s ⁻¹)	8.2	9.4	9.7	8.7	7.9	8.5	8.9 \pm 3.3	5.7	7.8	5.9	5.4	4.3	6.7	6.0 \pm 3.4
Ω	0.16	0.21	0.23	0.18	0.12	0.09	0.18	0.17	0.27	0.17	0.15	0.15	0.12	0.18

Table 3. Monthly total net radiation, mean bowen ratio, total evapotranspiration, mean ratio of precipitation to E_T , mean Priestley-Taylor coefficient, and mean midday CO₂ flux, water use efficiency, canopy conductance and canopy decoupling coefficient at Early Seral North and old-growth forest in 2006. Bolded values show site significant differences at $P < 0.001$.

2007	Early Seral South					Old-Growth				
	May	June	July	Aug	May-Aug	May	June	July	Aug	May-Aug
R_n (MJ m ⁻² mo ⁻¹)	408	361	435	368	393	494	445	523	411	468
β ($H/\lambda E$)	1.28	0.82	0.94	1.36	1.10 \pm 0.65	2.58	1.94	2.22	2.20	2.23 \pm 0.71
E_T (mm mo ⁻¹)	68	78	85	58	289 \pm 14	53	64	63	51	230 \pm 11
P/E_T	0.51	0.38	0.22	0.27	0.35	0.65	0.47	0.29	0.30	0.43
α (E_{Teq}/E_T)	0.53	0.63	0.57	0.52	0.56	0.43	0.46	0.39	0.40	0.42
F_{NEE} (μ mol m ⁻² s ⁻¹)	-4.6	-8.7	-7.2	-6.5	-6.7 \pm 1.0	-10.4	-10.8	-5.7	-7.9	-8.7 \pm 2.7
WUE (g C kg H ₂ O ⁻¹)	1.1	1.8	1.5	1.8	1.5 \pm 0.7	2.5	2.3	1.9	2.1	2.2 \pm 1.0
G_c (mm s ⁻¹)	6.1	7.1	5.4	5.0	5.8 \pm 2.7	6.2	6.9	5.0	5.7	5.9 \pm 4.0
Ω	0.15	0.21	0.16	0.13	0.16	0.31	0.33	0.31	0.29	0.31

Table 4. Monthly total net radiation, mean bowen ratio, total evapotranspiration, mean ratio of precipitation to E_T , mean Priestley-Taylor coefficient, and mean midday CO₂ flux, water use efficiency, canopy conductance and canopy decoupling coefficient at Early Seral South and old-growth forest in 2007. Bolded values show site significant differences at $P < 0.001$.

1 **Figure Headings**

2 1. Monthly diurnal plots of sensible heat (a), latent energy (b) and carbon dioxide flux
3 (c) at ESN and OG in 2006. The boxes highlight that site differences in ecosystem fluxes
4 change dramatically from May to July.

5
6 2. Monthly diurnal plots of sensible heat (a), latent energy (b) and carbon dioxide flux
7 (c) at ESS and OG in 2007. The boxes highlight that site differences in April were
8 greatest for CO₂ flux and in July for energy fluxes.

9
10 3. Time series of daily maximum δe and total E_T at ESS and OG during the seasonal
11 drought period in 2007. The circled points show two peaks in δe in June and August at
12 ESS and illustrate that δe is largely greater at the early seral stand than at OG.
13 Corresponding to the same two days, the squares show that E_T was two times greater at
14 ESS than OG in June but no large E_T difference was observed on the selected day in
15 August even though δe was 1 kPa higher at ESS.

16
17 4. Relationship between daily maximum δe and daily total E_T in June at ESN and OG (a)
18 and ESS and OG (c) and in August at ESN and OG (b) and ESS and OG (d). Daily E_T
19 was not correlated to vapor pressure deficit at the beginning of the summer at the old-
20 growth stand but a correlation was found between the two variables at the end of the
21 summer. At the early seral stands, a significant correlation was found during both
22 months.

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5. Daily mean Priestley-Taylor coefficient and relative soil water content grouped by month at the Early Seral North (a) and Early Seral South (b). Although θ_r was relatively high at ESS, α tended to be lower at this site. A θ_r threshold is clearly visible in the ESN data, available water content $< 30\%$ ($\theta_r = 0.3$) lead to a sharp decline actual E_T as compared to the equilibrium E_T or low α values.

6. Average canopy conductance by site and month for the hours of 8:00 until 15:30. Overall, G_c was higher in 2006 than in 2007 and greater at the early seral sites than at the old-growth stand during the afternoon hours.

7. A close examination of mean canopy conductance in May (a) and July (b) at ESS and OG in 2007. The arrows highlight three half hours showing the differences in morning, midday and afternoon G_c among stands at the beginning of the drought season (May) and in the middle of the drought season (July).

8. Mean midday canopy conductance binned by vapor pressure deficit in May-June (a) and July-August (b) at ESS and OG. G_c decreases logarithmically with increasing δe at all three sites. At the old-growth stand, G_c is significantly greater between 0 and 1 kPa than at either early seral stand but as δe reaches 2 kPa, G_c is systematically lower at the mature forest.

9. Canopy conductance at ESS and OG grouped by δe bins (0.5 kPa intervals from 0.5 to 4.5 kPa) at the beginning (a) and middle (b) of the 2007 drought season. G_c decreases

1 with increasing δe so that the lowest δe bins are found at the top-right of the figure
2 (starting at 0.5 kPa) and increase along the fitted lines to a maximum δe level (up to 4.5
3 kPa) in the bottom-left of the figure. The gray-filled symbols show mean G_c at each site
4 at the four highest vapor pressure deficit levels per drought-period. Bolded δe bins
5 correspond to May-June data and the dotted line represents a 1:1 fit.

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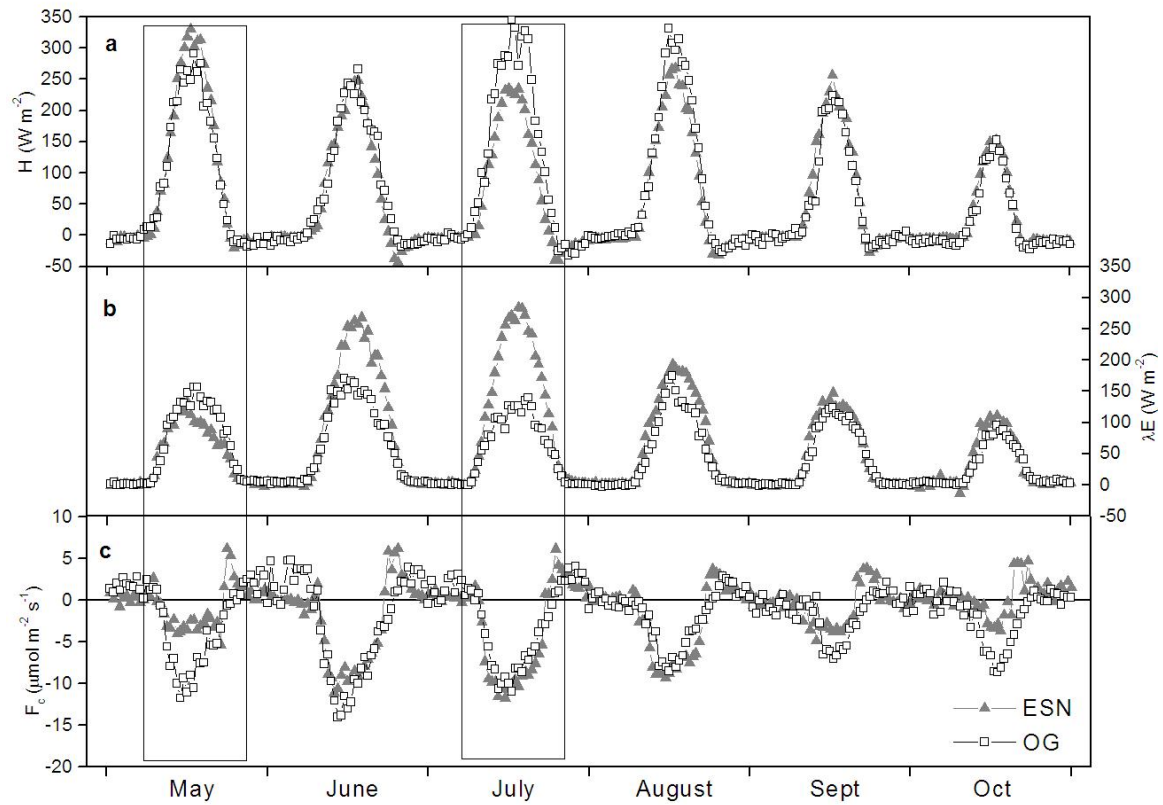
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1 **Figures**

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4 **Fig. 1**

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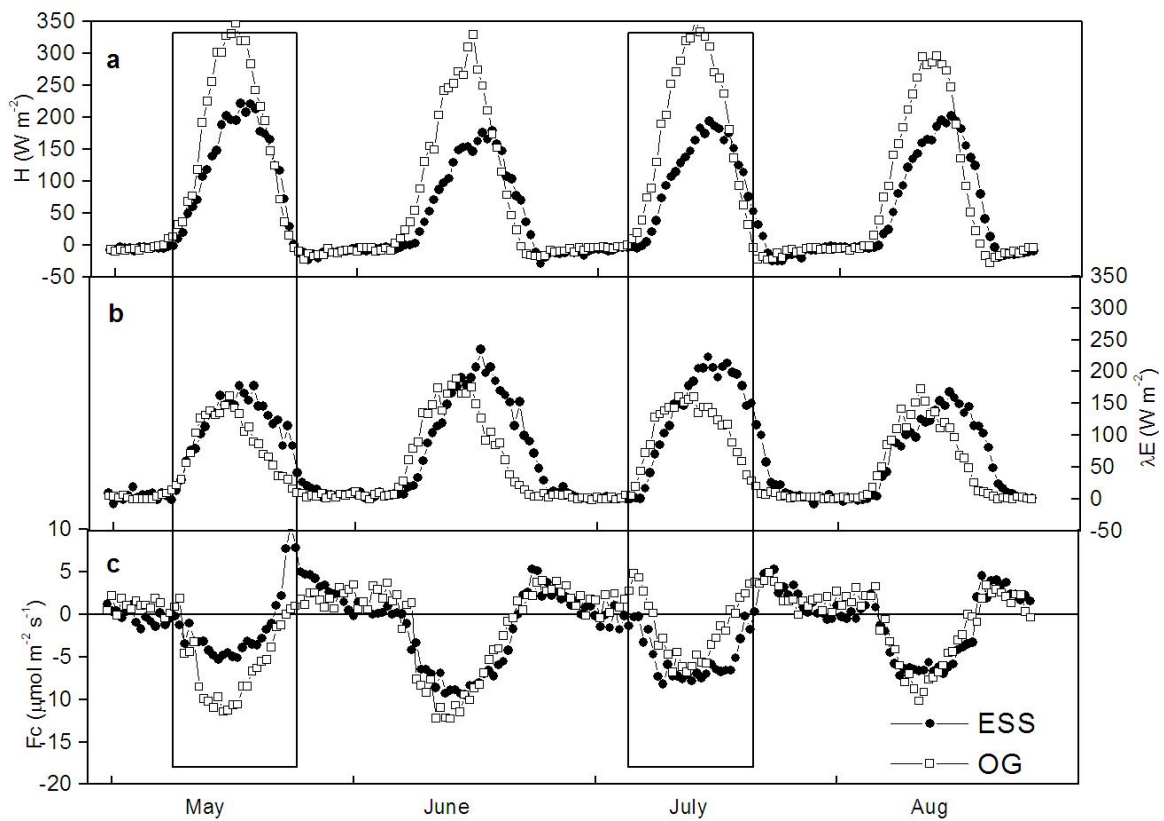


Fig. 2

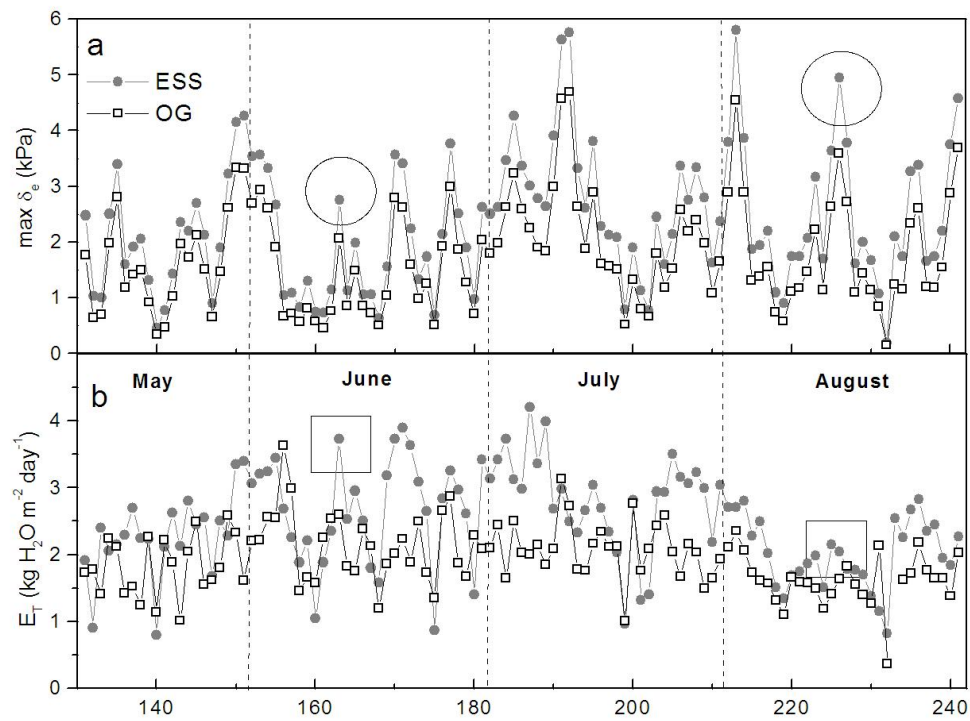


Fig. 3

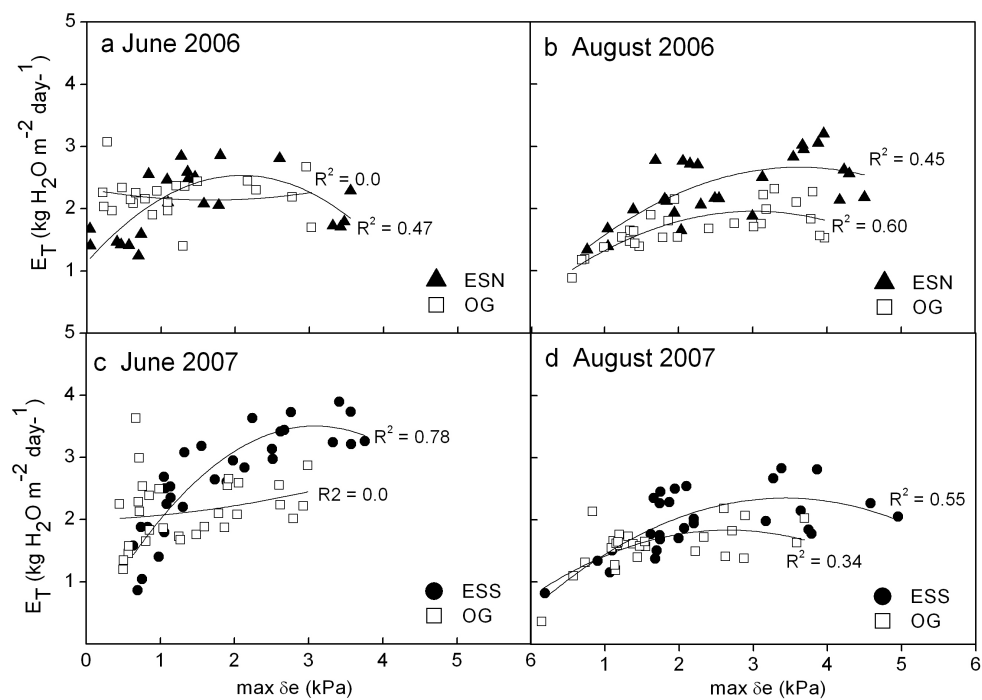


Fig. 4

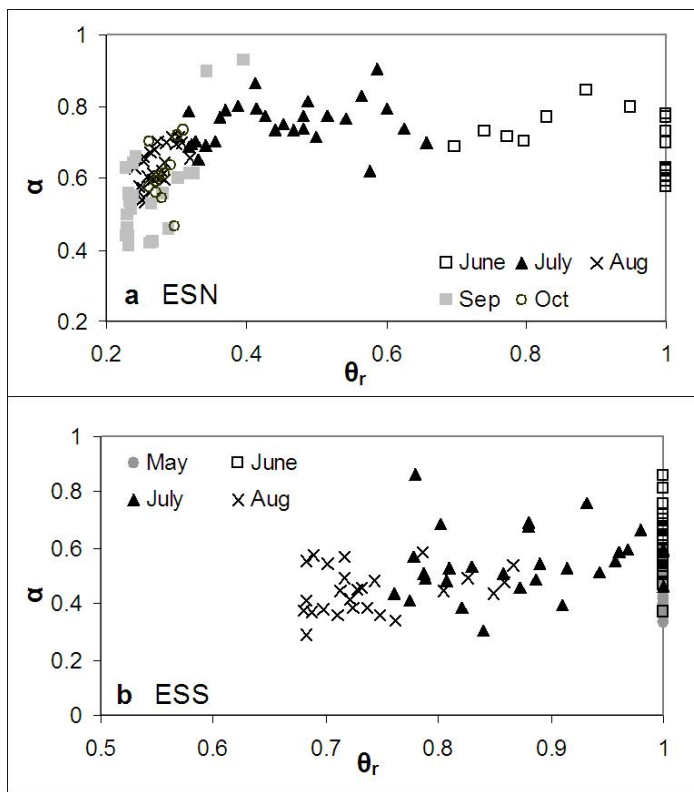
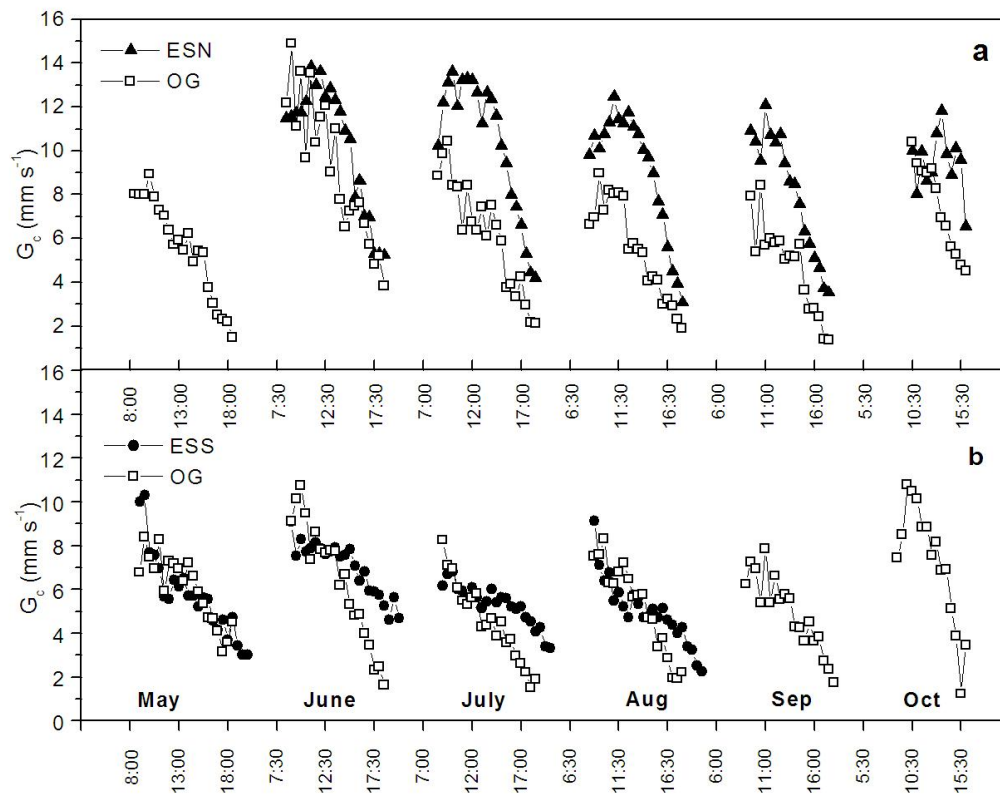


Fig. 5

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3 **Fig. 6**

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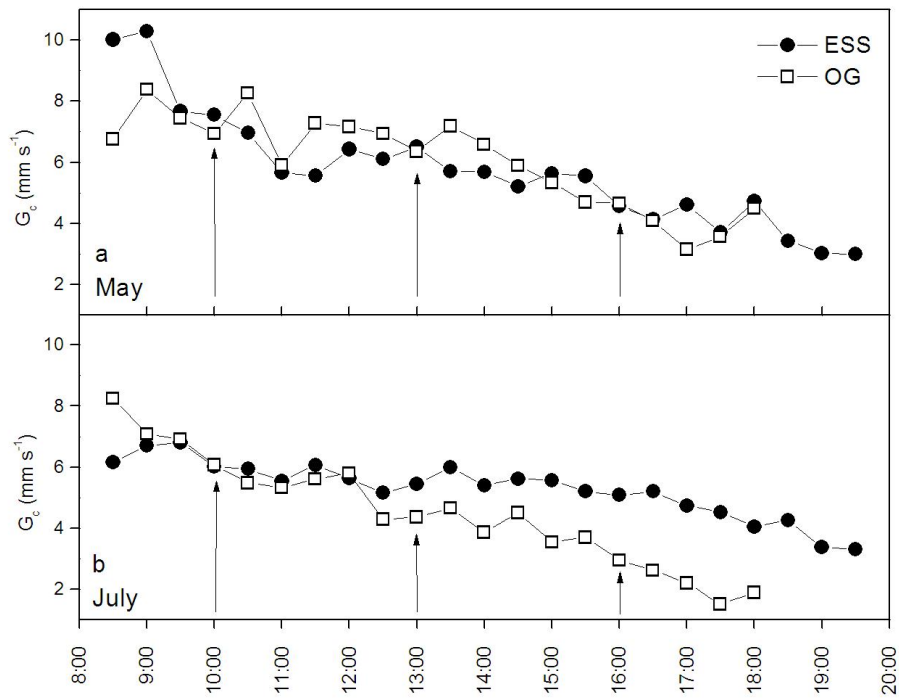


Fig. 7

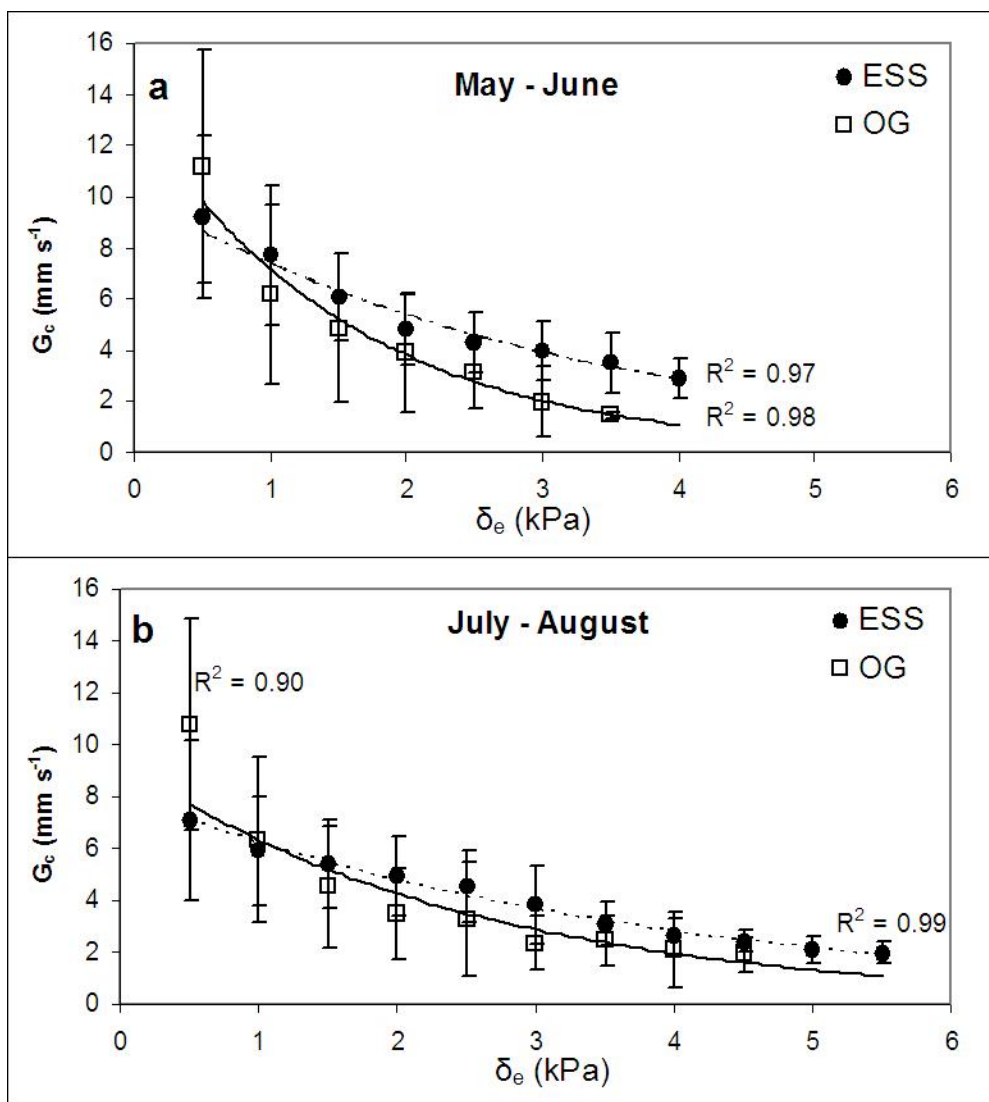


Fig. 8

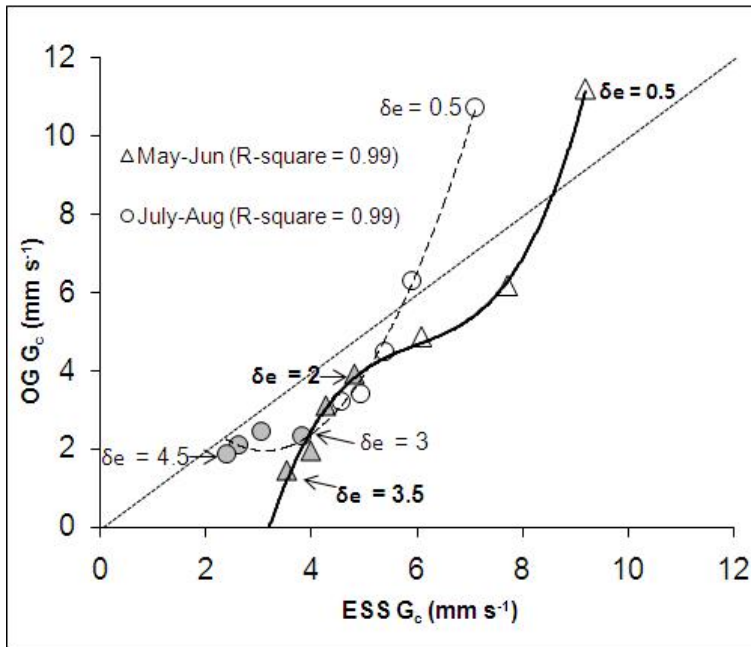


Fig. 9